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Linking functional traits to impacts of invasive plant species: a case study

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Abstract Our understanding of the link between plant functional traits and ecological impact of invasive alien plant species is fragmentary and the mechanisms leading to impacts are poorly understood. Moreover, current knowledge is heavily biased to the temperate regions of the world and we know much less about traits and impacts of invaders in tropical and subtropical ecosystems. We studied two leaf traits of the invasive alien shrub *Chromolaena odorata* and the impacts of its invasion on native vegetation in savannas. We compared specific leaf area (SLA) and leaf area index (LAI) between *C. odorata* and native species and assessed how *C. odorata* differentially affects canopy light interception, soil moisture, soil nutrients, and litter accumulation compared to native species. We found that *C. odorata* has higher SLA and LAI than native species, lower light and moisture levels below its canopy, but higher nutrient levels and a higher litter accumulation rate. Because of its higher SLA, *C. odorata* grows faster, resulting in more biomass, increased litter accumulation and higher nutrient availability. Due to its high SLA and LAI, *C. odorata* intercepts more light and reduces available moisture more than do native trees due to higher transpiration rates, reducing the biomass of native understory vegetation. This study provides empirical evidence for strong links between plant functional traits and ecological impact of invasive plant species, highlighting the importance of traits in predicting ecosystem-level impacts of invasive plant species.

Keywords Plant invasions · Functional traits · LAI · Leaf area · Litter · Savanna · SLA · Relative growth rate

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Introduction

Biological invasions are taking place globally at unprecedented rates, causing significant ecosystem-level impacts (Vilà et al. 2011). Understanding the role of functional traits is crucial for explaining links between species and ecosystem processes (Eviner and Chapin 2003; Diaz et al. 2013). However, whereas

traits related to invasion success are well studied ('response traits', e.g. Rejmánek et al. 2005; Pyšek and Richardson 2007; van Kleunen et al. 2010; Diaz et al. 2013), our understanding of the link between traits and impact is fragmentary and case-specific (Drenovsky et al. 2012; Pyšek et al. 2012; Diaz et al. 2013; Kumschick et al. 2015). Moreover, the literature is heavily biased towards the temperate regions of the world and we know much less about traits and impacts of invaders in tropical ecosystems, including savannas, which could limit progress in our understanding of plant invasions (Pyšek et al. 2008).

We studied the invasion of *Chromolaena odorata* (L.) King & Robinson, also known as Triffid weed or Siam weed, in South African mesic savannas (>650 mm annual rainfall). This species is widely regarded as one of the worst tropical shrub invaders, together with *Lantana camara* L. (Rejmánek and Richardson 2013), and is amongst the most prominent invaders of southern African savannas (Foxcroft et al. 2010). The species is native to South and Central America and has invaded most of the Paleotropics (Raimundo et al. 2007). It forms dense and impenetrable monospecific stands up to 2 m tall and invades not only anthropogenically modified habitats such as road verges and abandoned agricultural fields (Aboh et al. 2008), but also a wide variety of natural habitats, ranging from tropical rainforests to savannas (Macdonald and Frame 1988). In South African mesic savannas, *C. odorata* has major impacts on native ecosystems by out-shading native vegetation and excluding animals from invaded areas (Goodall and Erasmus 1996), but empirical evidence is largely lacking.

An increasing body of research shows that single invasive species can alter ecosystem processes and affect whole ecosystems (Ehrenfeld 2010; Hulme et al. 2013). However, since these effects are often strongly context dependent and variable, the impact of invasive species is often difficult to quantify and, therefore, generalize (Vilà et al. 2011; Pyšek et al. 2012). This has resulted in a limited number of quantitative impact studies—most of them focusing on temperate species (Hulme et al. 2013; Gaertner et al. 2014). The first attempts to develop a framework to quantify invader impact were made by Parker et al. (1999), who defined impact as a function of the area invaded (range), the invader abundance and its local effect ($I = R \times A \times E$). Impacts of invasive plants include species-level (e.g. hybridization with native species), community-level (e.g. reduction in biodiversity) and ecosystem-level impacts (e.g. changing resource dynamics, habitat structure, disturbance regimes, or impacting food webs).

Impacts arise due to the combination of traits that affect ecosystem processes and at the same time influence invader abundance (Drenovsky et al. 2012). The impact of invasive species is generally greatest when an invasive species adds a novel function or trait to an ecosystem, such as nitrogen-fixing ability (Yelenik et al. 2004) or different fuel properties (Brooks et al. 2004). However, the mechanisms by which impacts arise are generally poorly understood (Drenovsky et al. 2012). One of the most commonly reported traits in the literature is specific leaf area, SLA, and its inverse—leaf dry mass per area, LMA (Drenovsky et al. 2012). Specific leaf area has frequently been reported to influence invasiveness, where alien plants generally have greater SLA than non-invasive alien species (Rejmánek et al. 2005, but see Grotkopp et al. 2010). Specific leaf area positively correlates with relative growth rate (RGR), photosynthetic rate and leaf N, and negatively correlates with leaf lifespan (Westoby et al. 2002; Wright et al. 2004). It is also one of the key traits in the 'leaf economics spectrum' (Wright et al. 2004) that shows that variation in leaf traits is central to variation in plant ecological strategies (Westoby et al. 2002). A plant trait that is closely linked to SLA is leaf area index (LAI), which is a measure of leaf area per unit ground surface area (Niinemets 2010). This is not a trait of an individual leaf, but rather an index of light availability penetrating the whole canopy and, as such, is influenced by variation in plant height, canopy morphology, leaf thickness (SLA) and leaf area. Leaf area index both determines the shading effects of a plant on its neighbours and the extent to which water evaporates from leaves compared to the moist soil surface (Kelliher et al. 1995).

We studied two leaf traits of the invasive shrub *C. odorata* and the impacts of its invasion on native vegetation in savannas. We focused on mechanisms related to resource competition (light, moisture and nutrients) and litter accumulation. Our objectives were threefold: (1) to compare SLA and LAI between *C. odorata* and co-occurring native woody species; (2) to assess the impact of *C. odorata* on its environment, specifically on canopy light interception, soil moisture, soil nutrients and litter accumulation, in comparison to native woody species; and (3) mechanistically link

SLA and LAI to *C. odorata* impact in a conceptual framework.

Methods

Study species

Chromolaena odorata is perennial, semi-lignified shrub, averaging 1.5–2 m in height and reaching up to 6 m as a climber on other plants. Due to this specific growth form, *C. odorata* acts as a fire ladder in fire-prone savannas to catalyse canopy fires (Macdonald and Frame 1988; Te Beest et al. 2012). *Chromolaena odorata* is known to be deciduous under dry conditions—dying back, then resprouting from the living stem-base when conditions become more favourable. This strategy results in impenetrable shrubs with many dead and dry stems that form a physical barrier to humans and animals as well as increasing fire hazard in fire-sensitive habitats like gallery and riverine forests (Macdonald and Frame 1988; Goodall and Erasmus 1996). The invasion success of *C. odorata* is thought to depend on the combination of its high reproductive capacity, high relative growth rate and net assimilation rate (Ramakrishnan and Vitousek 1989) and its capacity to suppress native vegetation through light competition (Honu and Dang 2000; Feng et al. 2007). The species can reproduce apomictically and produces very large numbers of wind-dispersed seeds (a single shrub producing as many as 800,000 seeds; Witkowski and Wilson 2001). Also, the species sprouts prolifically and can survive severe disturbances like fire or cutting, and resist abiotic stress, especially droughts, by quickly re-growing from basal stems (Te Beest et al. 2012). *Chromolaena odorata* has been shown to exhibit allelopathic properties (Ambika 2002a; Qin et al. 2013) and alters soil biotic processes (Mangla and Inderjit 2008; Te Beest et al. 2009). In South Africa, this species is highly invasive in mesic savannas, where it seems to thrive under different climatic conditions than in its native range (Robertson et al. 2008; Te Beest et al. 2013).

Study area

Our study was performed in Hluhluwe-iMfolozi Park (HiP, 28°00′–28°26′ S, 31°43′–32°09′ E), a 90,000 ha reserve in Kwazulu-Natal, South Africa, within the southern African savanna biome. *Chromolaena odorata* was first recorded in HiP in the 1960s, and at the time of our study (2003–2006) it was the most dominant and widespread invasive species in the reserve, covering about 20 % of the northern part (Hluhluwe) with dense monospecific stands (Howison 2009). Up to 2004 no extensive management of *C. odorata* had been carried out. In 2004, a large-scale and labour-intensive control program was set up following the template of the national Working for Water programme (Van Wilgen et al. 1998). *Chromolaena odorata* densities were effectively reduced over the last 10 years (Te Beest, unpubl. data). For our studies, we specifically selected areas that had not yet been cleared. All studies, except for the soil nutrient transects, were carried out in the northern part of the reserve that received 540 mm of rain in 2003, 915 mm in 2004, 781 mm in 2005 and 990 mm in 2006 (data from Ezemvelo KZN Wildlife Scientific Services). The long-term average rainfall in HiP is approximately 800 mm/year and is strongly seasonal with most rain falling in summer between October and March (Balfour and Howison 2001). In the dry season (May–Aug), average monthly rainfall varies between 0 and 30 mm. Native woody species are adapted to survive these periods of low rainfall either by being deciduous (shedding their leaves during the dry season) or by maintaining morphological and/or physiological adaptations to endure droughts, such as extensive root systems and thick sturdy leaves with low SLA (Poorter and Markesteijn 2008; Tomlinson et al. 2012). With this amount of rainfall, savannas can be either dominated by grasses or trees, the local tree cover being determined by the amount of top-down control by herbivores and fire (Sankaran et al. 2005). The northern part of HiP, therefore, represents a mosaic of habitats from open grassland to closed woodland, with patches of subtropical forests, classified as scarp forests, in the absence of fire (Whateley and Porter 1983).

Specific leaf area

In July 2005, we measured leaf traits of *C. odorata* and native woody species across the northern section of the reserve (Hluhluwe). Specific leaf area was measured for 49 woody species, including *C. odorata*. Native woody species can be categorized into two functional

groups: broadleaved and fine-leaved species. The latter group is characterized by compound leaves and all belong to the legume families. For each species, we collected a sample of 3–5 leaves. Fresh leaves were kept in a plastic bag and photographed under a glass plate on the same day. Each sample was then dried in an oven at 70 °C for 48 h and weighed. Leaf area was measured from the photographs using the program Sigmascan Pro 5.0 (SPSS Inc.). Specific leaf area was calculated as leaf area divided by dry weight. We used a univariate ANOVA to test if the SLA of *C. odorata* differed from that of either of the two native woody species groups.

Leaf area index, light penetration and below-canopy grass biomass

In February 2006, we determined leaf area index (LAI) and % light penetration through the canopy using an AccuPAR LP-80 PAR ceptometer (Decagon Devices, Inc.). The LP-80 ceptometer measures photosynthetically active radiation (PAR) in plant canopies and calculates LAI based on above- and below-canopy measurements, allowing for rapid and non-destructive sampling. We measured 233 individual woody species: 104 broadleaved, 62 fine-leaved and 67 *C. odorata* shrubs, covering 21 different species. Additionally, for each individual woody species, we measured their height using a 2 m-pole and below-canopy grass biomass (including forbs) using a disc pasture meter (DPM, Bransby and Tainton 1977)—a metal disc (diameter 45 cm, weight 1,500 g) dropped from a standard height along a pole with a centimeter scale. This height measurement has been standardized and is generally used as a proxy for grass biomass, for example to assess fuel loads in savannas. In a paired sample, we measured grass biomass (DPM) in an adjacent patch away from the canopy to determine the ability of different woody species to negatively impact native grasses via competitive effects. To quantify this, we calculated relative competition intensities (RCI) as $(DPM_{open}–DPM_{below})/DPM_{open}$ (Weigelt and Jolliffe 2003). In an independent dataset that we collected in April 2006, we determined LAI using an LAI-2000 Plant Canopy Analyser (LI-COR, Inc.) that uses a fish-eye optical sensor rather than a series of linear photosensors. We measured 237 individuals, of which 157 were broadleaved, 56 fine-leaved and 23 *C. odorata* shrubs, covering 26 different species. We tested for differences in LAI, light penetration, below-canopy grass biomass and RCI using a mixed-effects model with functional group (broadleaved, fine-leaved and *C. odorata*) as fixed predictor variable and species as a random variable to account for the within-species variation.

Soil moisture

Soil moisture was measured in an experimental set-up for 3 months in the Sitezi area of northern Hluhluwe between April and June 2005. We aimed to separate effects of soil evaporation and plant transpiration to assess the water-use of *C. odorata* in a natural field setting. An open savanna site that was heavily invaded by *C. odorata*, but where the species had not yet formed a dense monoculture, was selected for the study. Dominant native grass species were *Panicum maximum*, *Sporobolus pyrimidalis*, *Themeda triandra* and *Eragrostis curvula*. Dominant native shrubs and trees were *Dicrostachys cinerea*, *Euclea divinorum*, *Phyllanthus reticulatus* and *Gymnosporia buxifolia*.

We established 4 plots of 2 × 2 m according to a randomized block design which we replicated 6 times. Blocks comprised (1) plots with intact *C. odorata* stands—*C. odorata* controls, (2) plots where we bent away the *C. odorata* using ropes and iron pins to expose bare soil to evaporation, but to minimize changes in plant transpiration—*C. odorata* bent, (3) plots which we cleared from all *C. odorata* shrubs—*C. odorata* cleared, and (4) plots with intact native vegetation. We compared 1 vs. 2 as a measure of evaporation, 1–2 vs. 3 as a measure of transpiration, and 1–3 vs. 4 to look at native vs. alien impacts.

We measured volumetric soil moisture content once a week using a ThetaProbe soil moisture meter (Delta-T Devices Ltd) that measures volumetric moisture content in the top 10 cm. This resulted in nine replicate measurements over the course of the experiment. Five replicate measurements were taken at random places within each 2 × 2 m plot and averaged per plot. To test for differences in soil moisture between experimental treatments, we used a mixed-effects model with experimental treatment as fixed predictor variable and block and date as random variables. We nested block within date to account for spatial and temporal pseudoreplication and performed Tukey tests to analyse differences between treatment levels (control, bent, cleared, native vegetation).

Soil nutrients

We measured *C. odorata* density and collected soil samples on 112, 100 m-long transects across the entire reserve from May to September 2004. The transects were located in open savanna and spanned the whole gradient of *C. odorata* density. There were 56 transects without *C. odorata*, and 56 transects with *C. odorata*, ranging from low density ($n = 37$), which was defined as less than 25 % cover of *C. odorata* (approximating <1 stem/m^2) to high-density monospecific stands with up to 100 % cover ($n = 19$). Soil cores were collected every 10 m along the 100 m transect from the topsoil (upper 10 cm) and bulked per transect. Samples were oven dried at 120 °C and send to the soil laboratory at Cedara, KZN, South Africa. The samples were analysed for total carbon (C) and nitrogen (N), exchangeable calcium (Ca), magnesium (Mg) and potassium (K), sodium (Na), soil pH and cation exchange capacity (EC). Data were analysed with univariate ANOVA with *C. odorata* density as the predictor variable, using Tukey tests to analyse differences between invasion levels (*C. odorata* absent, low density, high density).

Litter accumulation

We used a line-intercept method to assess vegetation and litter cover in 12 replicate plots along a gradient in *C. odorata* density in the Maphumulo area of northern Hluhluwe. These plots were part of an experiment to test the effect of fire and clear cutting on the control of *C. odorata* (Te Beest et al. 2012). To assess litter accumulation, we used the initial data collection in August 2003 before the experimental treatments were carried out. We laid out three 50 m line transects per plot, each spaced 10 m apart. On these line transects, we recorded vegetation and litter cover directly under the measuring tape at every meter, resulting in 150 points per plot, covering an area of 50 × 20 m. The litter of native trees and *C. odorata* is very distinct and therefore easy to differentiate. We classified vegetation and litter cover into the following groups: *C. odorata* shrub, native shrub or tree, *C. odorata* litter, native species litter, bare soil and grass. We tested for an effect of species (native vs. *C. odorata*) and shrub cover on litter cover. The difference in litter accumulation rate between native species and *C. odorata* is expressed in the strength of the interaction term (species × shrub cover). We tested for the significance of this interaction term by comparing the full model, including species, shrub cover and their interaction to the model without the interaction using a likelihood ratio Chi-square tests (Crawley 2007). All analyses were performed in the statistical environment R version 2.10.0 (2009-10-26) (R Development Core Team 2009).

Results

Specific leaf area

Chromolaena odorata has a high SLA (267 cm^2/g), which is on average more than double that of the native woody species that we measured (Fig. 1). Both broadleaved and fine-leaved savanna trees typically had an average SLA of around 100 cm^2/g ($F_{2,46} = 27.1$, $p < 0.001$).

LAI, light penetration and below-canopy grass biomass

The average LAI of all native woody species was 2.2. Broadleaved species had an LAI of 2.3, fine-leaved species an LAI of 1.9. On average, the LAI of *C. odorata* was higher than the LAI of both broadleaved and fine-leaved woody species with a value of 2.9 ($F_{2,18} = 6.54$, $p = 0.007$, Fig. 2a). Only two native woody species had higher leaf area indices: *Dombeya burgessiae* (3.5) and *Spirostachys africana* (3). The LAI of *Ziziphus mucronata* (2.9) was similar to *C. odorata*. We found no significant difference in LAI between broadleaved and fine-leaved native species. The independently collected LAI dataset shows strikingly similar LAI values for broadleaved trees (2.2), fine-leaved trees (1.5) and *C. odorata* (2.9), showing the consistency of the trait among functional groups. The average height for each functional group was 1.9 m (±0.3 m) for *C. odorata*, 3.5 m (±1.6 m) for fine-leaved trees and 4.4 m (±2.2 m) for broadleaved trees.

Light penetrating through the canopy was lowest under *C. odorata* shrubs, with only 18 % of light penetrating. This equates to a more than 80 % reduction in PAR, and results in a biomass reduction of native grasses of 45 % compared to an adjacent open patch. The percentage light penetrating through the canopies of broadleaved species was 23 %,

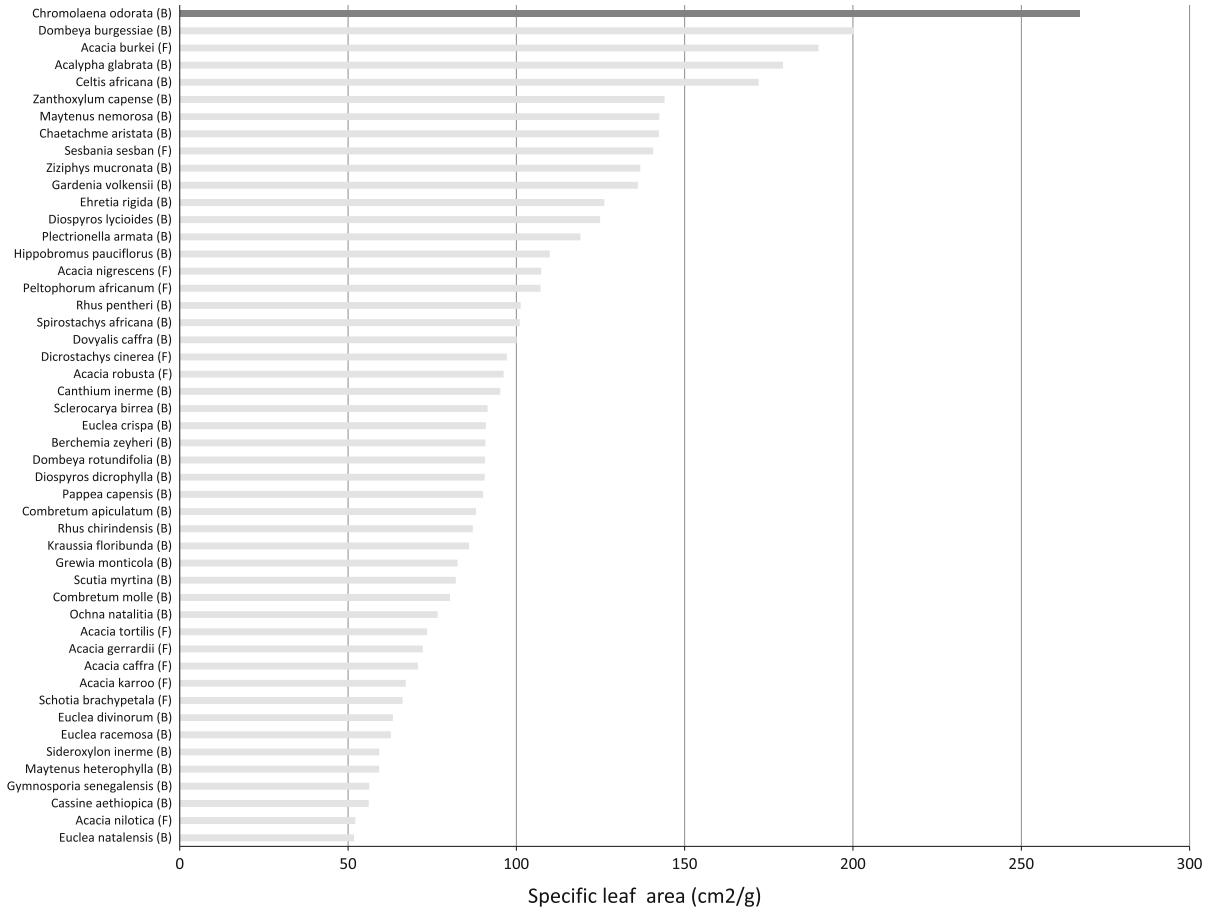

Fig. 1 Specific leaf area (SLA) per species for a selection of 49 common native savanna trees and the invasive alien shrub *Chromolaena odorata*

resulting in a 30 % grass biomass reduction compared to an adjacent open patch. Fine-leaved species such as *Dicrostachys cinerea* had a much smaller shading effect, with on average 30 % of the available light penetrating through the canopy ($F_{2,18} = 6.78$, $p = 0.006$, Fig. 2b), resulting in a reduction in grass biomass of only 5 %. Considering the shading effect of native species as part of normal savanna functioning, then the shading effect of *C. odorata* is more than double that of native species in terms of reduction of grass biomass. The relative competition intensity (RCI) shows the same result: *C. odorata* exerts the most intense competition for grasses together with broadleaved trees, while the fine-leaved trees have the lowest RCI ($F_{2,18} = 9.45$, $p = 0.002$, Fig. 2d).

Soil moisture

Soil moisture levels were lowest in the plots where *C. odorata* was either intact or bent and significantly higher in the plots with native vegetation or where *C. odorata* was cleared ($F_{3,24} = 25.80$, $p < 0.001$, Fig. 3). This indicates that dense stands of *C. odorata* (control treatments) dry out the soil, even when accounting for increased bare soil evaporation under *C. odorata* shrubs by bending the shoots away from the surface (bent treatment). Soil moisture levels under intact *C. odorata* shrubs were 4–5 % lower than in adjacent native vegetation. Once *C. odorata* was cleared, soil moisture levels went up to levels of the native vegetation.

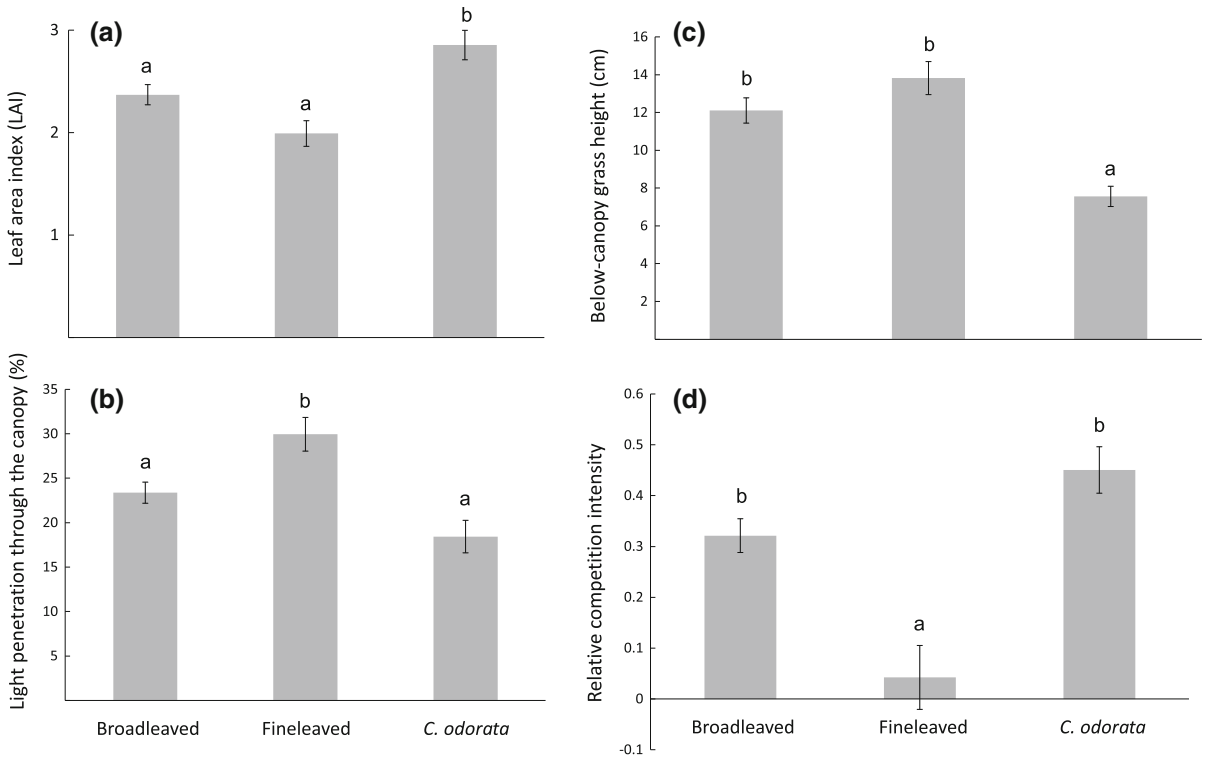

Fig. 2 **a** Leaf area index (LAI) per functional group: broad-leaved trees ($n = 104$), fine-leaved trees ($n = 62$), *Chromolaena odorata* ($n = 67$). **b** % light penetration through the canopy per functional group. **c** Below-canopy grass height (cm) per functional group. Grass height was measured with a disc pasture meter (DPM), which is generally used as a proxy for grass biomass. **d** Relative competition intensity, calculated as the proportional decrease in grass height (DPM) below the tree or shrub canopy as compared to an adjacent open patch

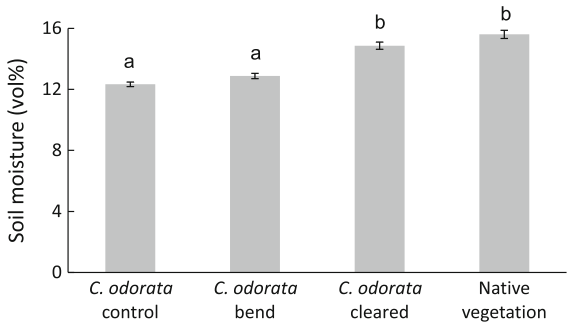

Fig. 3 *Bar plot* of soil moisture across different experimental treatments: a control *plot* with dense *C. odorata*, *C. odorata* shoots bent away from the surface of the plot, all *C. odorata* cleared (cut and removed) from the plot, and native vegetation

Soil nutrients

We found higher percentages of total carbon and nitrogen on transects with high-density *C. odorata* compared with low-density transects or transect where *C. odorata* was absent (C: $F_{2,109} = 23.03$, $p < 0.001$; N: $F_{2,109} = 19.00$, $p < 0.001$, Fig. 4). Exchangeable cations showed a more complex picture. Concentrations of Ca and Mg increased with increasing *C. odorata* density (Ca: $F_{2,109} = 19.10$, $p < 0.001$, Mg: $F_{2,109} = 12.39$, $p < 0.001$). Concentrations of Na and K, and soil pH (data not shown) did not differ between transects.

Litter accumulation

Chromolaena odorata had a high litter accumulation rate (slope $= 0.57, t = 6.53, p < 0.001$, Fig. 5), much higher than native trees and shrubs (species × shrub cover: $p = 0.004$). In high-density stands with a *C. odorata* cover of >50 %, up to 40 % of the soil was covered by a dense layer of *C. odorata* litter. For native shrub and trees, the amount of litter covering the soil (native litter input) did not depend on the cover of the native shrub and trees ($t = -0.3$, $p = 0.76$).

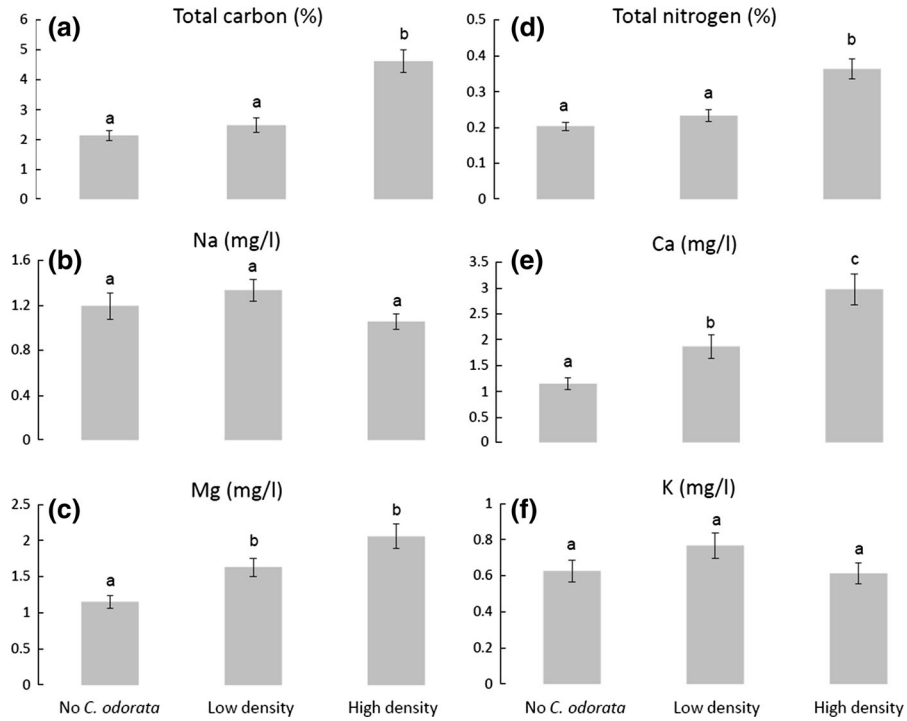

Fig. 4 Soil nutrient concentrations determined across 100 m transects with different *Chromolaena odorata* densities: no *C. odorata* present ($n = 56$), low density ($n = 37$) and high density ($n = 19$). The different graphs show concentrations of carbon (**a**), sodium (**b**), magnesium (**c**), nitrogen (**d**), calcium (**e**) and potassium (**f**)

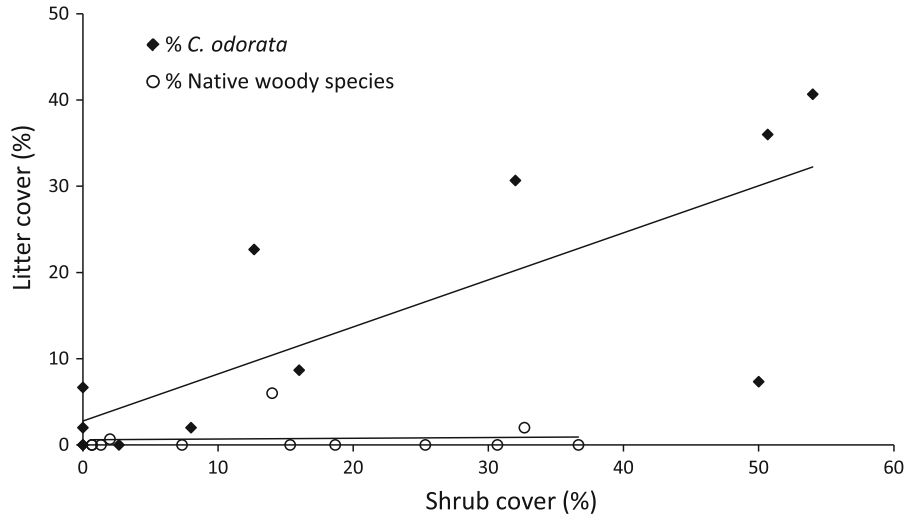

Fig. 5 Litter accumulation of *C. odorata* (*closed symbols*) and native tree and shrub species (*open symbols*) with fitted linear regressions

Discussion

A higher SLA results in faster growth rates (Wright et al. 2004), which leads to high biomass production and litter accumulation that in turn may affect nutrient accumulation (Chapin et al. 2011; Meisner et al. 2012), soil biotic processes (Mangla et al. 2008; Te Beest et al. 2009), and the fire regime (Te Beest et al. 2012). The combination of a high SLA and high LAI results in high transpiration rates (Kelliher et al. 1995; Niinemets 2010) that reduce available soil moisture, and allows for more efficient capture of light and out-shading of native vegetation. In savannas with a distinct dry season, native woody species have been

selected to cope with seasonal water stress, generally allocating more biomass to roots and having thick sturdy leaves with low SLA (Poorter and Markesteijn 2008; Tomlinson et al. 2012). We found the opposite for *C. odorata*. This invasive species has higher SLA and LAI than co-occurring native woody savanna species. In Fig. 6, we summarize the impacts of the invasion by *C. odorata* and its inter-linkages with SLA and LAI.

It has often been suggested that *C. odorata* is effective in reducing native vegetation through competition for light (Goodall and Erasmus 1996; Honu and Dang 2000). We now show empirically that *C. odorata* is indeed very effective in shading out native grass communities. *Chromolaena odorata* reduced light availability and grass biomass beneath its canopy to a greater extent than native woody species. Relative competition indices (RCI) that we calculated by comparing understory grass biomass with an adjacent open patch confirmed this. *Chromolaena odorata* had a higher RCI than fine-leaved woody species, but not than broadleaved woody species. We found that competition was not only mediated by light, but also by water. With our soil moisture experiment, we could show that *C. odorata* reduced available soil moisture below its canopy more than native vegetation did, and that plant transpiration (high LAI), rather than evaporation, determined the soil moisture levels beneath *C. odorata* canopies. However, we have to note that with our experimental design we were not able to separate the effects of transpiration and evaporation completely. Roots of plants outside the plots may have grown into the bent or cleared treatments and consuming soil water of these plots through transpiration. The high resource use by *C. odorata* is consistent with a strategy of rapid growth (high SLA). However, such a strategy can only be sustained on high-nutrient soils and this is indeed where we find the highest densities of *C. odorata*. This is in line with the 'try-harder' hypothesis of Tecco et al. (2010) which posits that alien woody species show more acquisitive attributes than native species in more resource-rich habitats. It is also in agreement with results of greenhouse studies that showed higher performance of *C. odorata* in high-nutrient soils (Li et al. 2012; Liao et al. 2013; Qin et al. 2013).

A recent paper by Diaz et al. (2013) shows the inherent link between species-specific traits and the effect of the species on its environment (specific effect functions, SEF). Due to its specific traits, *C. odorata* is able to express an ecological strategy that is characterized by rapid resource acquisition and depletion under favourable conditions. This 'reckless' ecological strategy (Simberloff and Gibbons, 2004) cannot be maintained when conditions become unfavourable, such as during seasonal droughts or after fire. In these conditions *C. odorata* dies back and depends on its sprouting capacity to re-grow when conditions become more favourable again. Therefore, temporally unfavourable conditions do not affect the long-term

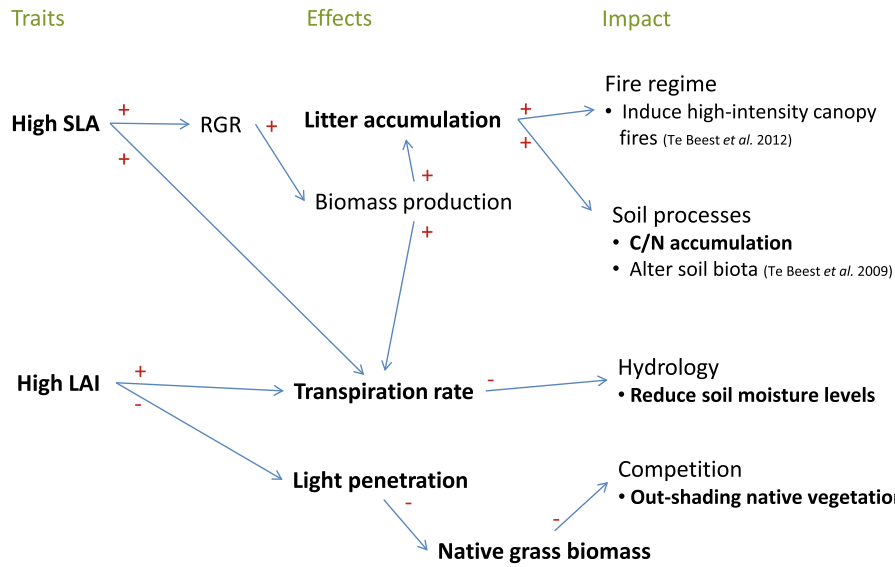

Fig. 6 Summarized links between SLA and LAI and ecosystem processes for *Chromolaena odorata* in Hluhluwe-iMfolozi Park, South Africa. "+" indicates positive effects; "−" indicates negative effects. In *bold text* interactions that are studied in this paper. In *normal text* interactions that have been shown in the literature. In *grey text* hypothesized interactions

persistence of *C. odorata* and its overall success as an invasive species. Other traits that play a role in the invasion success of *C. odorata* are the high propagule pressure of wind-dispersed seeds (Witkowski and Wilson 2001), the plasticity in biomass allocation and low root to shoot ratios (Te Beest et al. 2009, 2013; Liao et al. 2013), and the timing of seed set during the main fire season (July–October). We hypothesize that this might have been particularly important for the rapid spread of *C. odorata* in HiP. Fire eliminates the majority of *C. odorata* seeds in and on the soil (Witkowski and Wilson 2001; Te Beest et al. 2012). However, low to moderate-intensity grass-layer fires, which are common in prescribed savanna burns (Balfour and Howison, 2001; Govender et al. 2006), do not burn the top parts of the *C. odorata* plants where the seeds are located (MtB, pers. obs.). Therefore, if areas are burned during seedset of *C. odorata*, seeds will drop in fertile soils with no grass competition and will easily establish (Te Beest et al. 2014). The best timing for prescribed burns in invaded areas would be in the period after flowering but before seed set (July), when seeds will not have developed yet and plants will resprout less vigorously due to high investment of reserves in reproduction (Witkowski and Wilson, 2001).

Litter accumulation rates were higher for *C. odorata* than for native woody species. This litter consist mostly of stems, rather than leaves since *C. odorata* allocates the highest proportion of its biomass to stems (Ramakrishnan and Vitousek 1989; Te Beest et al. 2009, 2013). These stems are light and brittle and break easily (MtB, pers. obs.). We hypothesize that the elevated total C and N levels that we found in soils with high-density *C. odorata* can be (at least partly) attributed to this high litter fall. Previous research comparing a selection of temperate alien forbs with their native congeners has shown that increased soil nutrient availability can be attributed to high litter input (Meisner et al. 2012). The classic idea in ecosystem ecology is that fast growing species thrive in high-nutrient soils and their litter tends to decompose quickly, creating a positive feedback to high-nutrient soils (Liao et al. 2008; Ehrenfeld 2010; Chapin et al. 2011). Even though we measured total soil N, which is not a measure of soil N availability, the total N data is indicative of *C. odorata* redistributing resources to top soil layers. Altered litter dynamics can have cascading effects on ecosystem processes beyond short-term nutrient inputs in the soil. These effects may be long-lasting and difficult to reverse. For example, Eppinga et al. (2011) illustrate how altered litter dynamics caused by the invasive reed *Phalaris arundinacea* could induce a positive feedback where highly competitive *P. arundinacea* genotypes outcompete native species. This induced a critical transition from a low-litter, native-species-dominated state toward a high-litter, *P. arundinacea*-dominated state. Likewise, experimental studies with *C. odorata* have shown that high litter inputs increase its own seedling establishment, potentially inducing a similar positive feedback as described for *P. arundinacea*. In a common garden study *C. odorata* seedling emergence doubled on soil surfaces mulched with *C. odorata* twigs (Ambika 2002b) and in a field study seedling establishment was highest where *C. odorata* was experimentally cleared and the litter was left (Te Beest et al. 2012, 2014). Previous research has also shown effects of *C. odorata* on soil biota (Mangla and Inderjit 2008; Te Beest et al. 2009).

The high investment in light stem biomass in *C. odorata* may lead to yet another ecosystem-level effect, namely alteration of the fire regime. Due to its typical dense or scrambling growth form, the leaves are mostly situated on the outer branches, whereas the larger part of the shrub consists of an impenetrable network of stems. When the plant dies back due to a drought, the dried up stems remain as 'skeletons' in tree canopies. These dry stems (and leaves) are reportedly flammable (contain essential oils) (Muniappan and Viraktamath 1993; Witkowski and Wilson, 2001) and are able to lift ground fires into tree canopies, causing intense and highly destructive canopy fires that are not a normal part of savanna functioning (Macdonald and Frame 1988; Te Beest et al. 2012).

To summarize, we have shown that differences in species-specific traits between the invasive alien shrub *C. odorata* and native savanna trees and shrubs influence the impact of the invader. A higher SLA enables *C. odorata* to grow faster, produce more biomass and stem litter, resulting in higher nutrient levels. A higher SLA and LAI enables *C. odorata* to intercept more light and reduces available moisture more than do native trees due to higher transpiration rates, reducing the biomass of native understory vegetation. We are aware that since we measured only two leaf traits (SLA and LAI) in this study, the

results are difficult to generalize and that further work is needed to examine more traits and more species. Nevertheless, our study provides empirical evidence for strong links between plant functional traits and ecological impact of invasive plant species.

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